

The University of Chicago

**PENNSYLVANIA FLORA OF ILLINOIS
AS REVEALED IN COAL BALLS. I**

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
PHYSICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GEOLOGY AND PALEONTOLOGY

1933

By
ROY GRAHAM

Private Edition, Distributed by
**THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS**

Reprinted from
THE BOTANICAL GAZETTE
Vol. XCV, No. 3, 1934

The University of Chicago

PENNSYLVANIA FLORA OF ILLINOIS
AS REVEALED IN COAL BALLS. I

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
PHYSICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GEOLOGY AND PALEONTOLOGY

1933

By
ROY GRAHAM

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
THE BOTANICAL GAZETTE
Vol. XCV, No. 3, 1934



PENNSYLVANIAN FLORA OF ILLINOIS AS REVEALED IN COAL BALLS. I

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 451

ROY GRAHAM

(WITH PLATES VIII, IX AND TWENTY-SIX FIGURES)

Introduction

This paper is the result of studies made of fossil plants preserved in coal balls from Calhoun coal mine, Richland County, Illinois. The material was collected by Dr. A. C. NOÉ under the auspices of the Illinois State Geological Survey. The mine has now been abandoned, so that no more material can be collected there. The writer is much indebted to Dr. NOÉ, who kindly supplied the coal balls, and under whose direction the research was carried out.

The geologic horizon from which these petrifications were obtained is about Middle Conemaugh in age, and is near the top of the Pennsylvanian strata found in Illinois.

Thin sections of the material were prepared by employing almost exclusively the cellulose peel process (3). By the use of this method, ten sections of material could easily be obtained to the millimeter, such close sections being almost essential in the study of the small strobili and seeds in order to get sections through critical structures. The numbers of the preparations, as given in this paper, refer to slides in the University of Chicago paleobotanical collections.

Description of plants

FILICALES

Notoschizaea robusta gen. et sp. nov. (preparations 549-553)

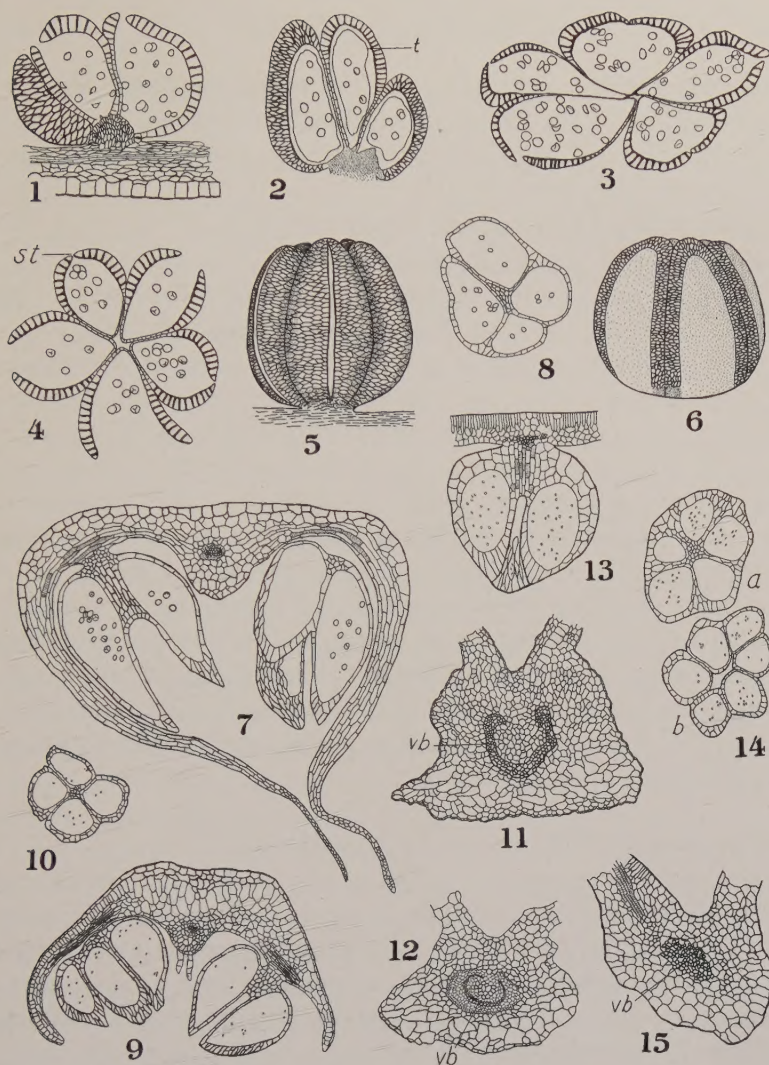
GENERIC DIAGNOSIS.—Sorus consisting of a circular group of sporangia which are so closely crowded as to resemble a synangium. Sporangia sessile, attached to the abaxial surface of a leaf by a narrow base, all of the sporangia of a sorus arising at a common point. Sporangia dehisce by means of a longitudinal cleft in the abaxial wall of the sporangium along a definite line (stomium). The outer

wall of the sporangium consists of heavy walled cells which form a wide annulus each side of the stomium.

SPECIFIC DIAGNOSIS.—Sporangia ovoid in shape, measuring about 1 mm. in length by 0.5 mm. in breadth and arranged in groups of five. Spores spherical, $55\ \mu$ in diameter, surface smooth and marked with a triradiate ridge.

This species is represented by preparations 549 to 553 in the University of Chicago collections. In preparations 551 and 552 there are excellent transverse sections of a sorus which has been slightly flattened as a result of pressure (figs. 3, 26). Five sporangia arranged in a circle make up the sorus. The sporangia are free from one another at the level of these sections but their lateral walls are flattened and in close contact. They measure about 0.5 mm. in diameter. The adjacent walls of the sporangia are thin but the outer walls are greatly thickened, measuring about $75\ \mu$ in thickness. There is a break in the continuity of the sporangium wall down the abaxial side, where dehiscence took place by means of a longitudinal cleft. On each side of this cleft the first cell (lip cell) is triangular in section, and is shorter in radial dimension than the other cells of the annulus. The apices of the triangular cells meet along the stomium. The whole of the abaxial wall of the sporangium is thus specialized to form an annulus (or more correctly, two annuli), one on each side of the stomium. The cells of the annulus are of the typical structure, with thickened inner and radial walls and a thin outer wall. Dehiscence is accomplished by the springing outward of the two annuli, thus opening a wide cleft along the stomium (fig. 4).

Preparations 552 and 553 contain obliquely longitudinal sections of the sori (figs. 1, 2). The sporangia are borne on the lower surface of a leaf and are attached thereto by means of a small common pad at their base. The sporangia are free from one another nearly to their bases. In 552 the sporangia have separated but those in 553 are closely appressed. This same state is shown in the transverse sections (figs. 3, 26) and it appears to be the normal position. In tangential section the cells of the sporangial wall are seen to be lozenge-shaped, with the long diagonal transverse to the axis of the sporangium. The cells measure about 70 by $30\ \mu$. There appears to have been a well marked tapetum present which is preserved as a



FIGS. 1-15.—Figs. 1-5, *Notoschizaea robusta*: 1, longitudinal oblique section of sorus attached to leaf lamina (552b); 2, longitudinal but somewhat tangential section of sorus (*t*, tapetum) (553); 3, transverse section of sorus (552a); 4, same of sorus restored. Two sporangia dehiscing (*st*, stomium); 5, restoration of sorus. $\times 22$. Fig. 6, *Corynopteris coralloides* (after ZEILLER) for comparison with *Sphaerotheca robusta*. $\times 20$. Fig. 7, *Scoleopteris latifolia*, cross-section of fertile pinnule bearing sporangia. Synangium on left is in median longitudinal section. $\times 22$. Fig. 8, cross-section of synangium of same near base. $\times 22$. Figs. 9-12, *S. minor*: 9, cross-section of fertile pinnule (523); 10, cross-section of synangium (520); 11, 12, cross-sections of ultimate rachis (*vb*, vascular bundle) (520, 524). $\times 22$. Figs. 13-15, *Cyathotrachus bulbaceus*: 13, longitudinal section of synangium (541); 14, cross-sections of two synangia (sectioned *a*, near base; *b*, near summit) (540); 15, cross-section of ultimate rachis (540). $\times 22$.

dark line slightly separated from the sporangium wall (fig. 2 t). The structure of the leaf upon which these sporangia are borne is not well preserved, but the upper epidermis is very thick and has a palisade-like structure.

The spores are spherical and measure about 50μ in diameter. The surface is marked by a triradiate ridge, but is otherwise smooth.

Having regard to the abaxial or dorsal dehiscence and to the robust sporangia, the name *Notoschizaea robusta* is proposed.

The individual sporangia of *Notoschizaea*, as far as the annulus is concerned, are much like those of *Etapteris*, in which there is a double, multiseriata, vertical annulus. The sporangia, however, are grouped in a circle in such a way as to resemble the synangium of *Scolecopteris* and related genera. *Notoschizaea*, like *Corynepteris*, combines characters of the Marattiaceae with those of the Zygopteridaceae. The resemblance to *Corynepteris* is very strong, and if the annuli of a *Corynepteris* were widened so as to occupy the whole of the abaxial surface of the sporangia, and the place of dehiscence changed from the ventral surface to the line of contact between the annuli, the resultant structure would be exactly as in *Notoschizaea* (figs. 5, 6). *Notoschizaea* is therefore placed provisionally with *Corynepteris* in the Zygopteridaceae.

***Scolecopteris latifolia* sp. nov.** (preparations 542-544)

DIAGNOSIS.—Sporangia three to four borne in pedicellate circular synangia; united laterally and attached to a central column for about half their length, free above. Outer wall of sporangium not thicker than the lateral walls. Sporangia 1.1 mm. long by 3.5 mm. in diameter. Spores 35μ in diameter. Leaves very broad and revolute, completely inclosing the sporangia.

The sporangia are borne in circular sori, three or four to a sorus. The sori are attached above lateral veins in a double series, one row each side of the midrib. The sori are pedicellate, the sporangia of a single sorus being attached to the pinnule by a common stalk which extends up the center of the sorus for nearly half the length of the sporangia. The sporangia are attached by their inner margins to this central column. Above the column they are free from one another (figs. 7, 27).

In shape the sporangia of *Scolecopteris latifolia* are ovate with a pointed end. In cross-section they are circular, except for the flattening where two sporangia are in contact (fig. 8). They measure about 1.1 mm. in length by 0.3–0.35 mm. in diameter. They are exannulate, and the sporangial walls are all of approximately the same thickness, about 20 μ , the outer wall not being thicker than the adjacent walls as is the case in *S. elegans* and *S. minor*. The walls consist of a single layer of platelike cells which are elongated in the direction of the axis of the sporangium. Dehiscence is by a longitudinal slit along the inner margin of the sporangium. The spores are much larger than those of either of the species previously described, being about 31 μ in diameter. Apart from the triradiate markings due to formation in tetrads, there are no special surface markings.

The sporangia are attached to the abaxial surface of leaf laminae. The pinnule is much revolute, the two margins almost meeting so as to inclose the sporangia. The pinnule if unrolled would measure about 7 mm. wide. The structure of the lamina of the leaf is poorly preserved, but from the various sections portions of all regions of the leaf may be made out. There is a thick upper epidermis and a rather thin and often indistinct lower epidermis, in which, however, stomata have been recognized. The mesophyll is without a distinct palisade layer. Between the point of attachment of the sporangia and the margin of the pinnule, the mesophyll consists of flattened plate-like cells. The vascular bundle of the midrib consists of a small circular bundle of tracheids surrounded by a narrow zone of disintegrated parenchyma, probably in part phloem. In the lamina below each sporangium is a mass of transfusion tissue (fig. 7). This is probably part of a lateral vein. No transfusion tissue occurs in the column which supports the sporangia.

The sporangia of this species have the characters of those of the genus, but this species is very distinct from the two hitherto described. In general size of the sporangia it resembles *S. elegans* but is slightly larger. It differs from both *S. elegans* and *S. minor* in the relatively greater development of the central column, in the lack of thickening of the outer wall of the sporangia, and in the larger spores. The greater breadth of the leaf lamina is also a feature. In the development of the central column it resembles *Acitheca*, from which it

differs in having pedicellate synangia and in the absence of the bristle-like acuminate tips to the sporangia.

On account of the broad lamina of the pinnule the name *Scoleopteris latifolia* is proposed for this species.

Scoleopteris minor Hoskins.

Fronds of the *Pecopteris* type, bearing shortly pedicellate circular sori on the lower surface of the pinnule in a double series, one row on each side of the mid-vein. Pinnules measure about 2.8 mm. long by 1.7 mm. wide. Sori are circular, composed of four or five exannulate sporangia attached to the short pedicel by their inferior-basal margins. Sporangia ovate, roughly circular in cross-section with adjacent sides slightly flattened; distal ends extended into slightly crescent acute apices by the elongation of the sporangial wall cells. Sporangia about 0.24 mm. in diameter by 0.57 mm. in length. Wall cells of the free surface much larger with heavier walls than those of the adjacent cells. Dehiscence occurs by means of a vertical cleft on the innermost wall of the sporangium. The spores are about $18\ \mu$ in diameter. The vascular bundle of the ultimate rachis is U-shaped with the ends of the arms slightly but abruptly involute (figs. 11, 32).

From several different coal balls, sections were obtained which give the structure of the ultimate rachis of a fernlike frond with pinnules bearing fructifications. The best of the material was obtained from two coal balls, C 210 and C 211B. The fern is so similar to that described by HOSKINS (5) as to leave little doubt as to its specific identity. There are, however, three minor differences from HOSKINS' material:

1. The pinnules are of smaller size, measuring only 2.8 mm. in length by 1.7 mm. in breadth, instead of 6–7 mm. in length by 3.3 mm. in breadth.
2. There is a well developed palisade layer in the leaf; HOSKINS' specimens had but poorly developed palisade tissue.
3. There is a wide variation in the structure of the ultimate rachis. One form (fig. 12) has a comparative weak vascular bundle surrounded by a zone of extremely thin walled parenchyma. At the other extreme the vascular bundle is much more robust and is not

surrounded by tissue different in any respect from the rest of the cortex (fig. 11). It is only the first type that HOSKINS described and figured.

These differences are modifications in vegetative structures, of the sort easily induced by environmental and other factors, and as such are not trustworthy criteria for building up taxonomic distinctions. The structural differences under (1) and (2) are possibly due to differences between a shaded environment in the case of HOSKINS' specimens and an exposed environment in the case of the specimens studied by the writer. The differences described under (3) may be due to the variation in the plane of the section. A rachis sectioned nearer the base will naturally show a larger vascular bundle and may also have other structural differences.

Cyathotrachus bulbaceus sp. nov. (preparations 535-541)

DIAGNOSIS.—Sporangia four to six, attached basi-laterally to a short central column, their bases completely united to form a saucer-shaped receptacle. The sporangia are united laterally for the greater part of their length by a common wall, a deep cup being left at the summit of the synangium. Synangia pedicellate and bulblike in shape, measuring about 0.65 mm. in diameter. Spores are 18 μ in diameter.

Preparations 535 to 541 contain sporangia attached to the under surface of a leaf lamina. There are longitudinal and transverse sections of the sporangia and obliquely transverse sections of the ultimate rachis. The sporangia are united into circular synangia similar to those of *Ptychocarpus*, but differing from that genus in several important respects.

The synangia are stalked, and each consists of from four to six sporangia united laterally at their bases to a short column which extends for about one-third the length of the sporangia, and also by a common envelope similar to but less highly developed than in *Ptychocarpus*. The uppermost parts of the sporangia are free although closely appressed (fig. 14 *b*); but nearer the base they are completely fused, the individual sporangium walls being completely merged into the common wall (fig. 14 *a*).

The sporangia are round in cross-section but are somewhat flat-

tened on their adjacent walls. In longitudinal section they are ovate in outline, with bluntly pointed tips (fig. 13). There is no annulus, but the cells of the outer wall and at the tip are larger than the others. Dehiscence probably occurred along the inner margin of the sporangia, the spores being discharged into the cup-shaped space lying between the sporangia at the summit of the synangium. The sporangia measure about 0.65 mm. long by 0.3–0.35 mm. wide. The synangia average 0.65 mm. in total diameter. The spores are round, about 18 μ in diameter, and show the characteristic tetrad markings.

In cross-section the leaf is seen to consist of an upper epidermis of platelike cells, an exceptionally well developed palisade layer consisting of much elongated prismatic cells, a spongy mesophyll, and a lower epidermis in which stomata have not been recognized with certainty (fig. 13). The synangia are attached above the secondary veins of the leaf. These veins consist of several tracheids accompanied by a much larger amount of transfusion tissue. This latter also extends into the column of the synangium but does not spread into the basal receptacle.

In the ultimate rachis (fig. 15) there is a central xylem bundle whose form appears to be elliptical in shape with the long axis parallel to the plane of the frond. The position of the protoxylem points could not be distinguished, but the tracheids are smaller on the adaxial side. Surrounding the xylem bundle is a narrow zone of exceedingly thin walled parenchyma (probably phloem), and outside this is the cortex which consists of larger cells with thicker walls. The largest cells of the cortex are found on the abaxial side of the rachis.

This sporangium is obviously closely related to those of *Cyathotrachus* and *Ptychocarpus*, with which it agrees in having a common envelope to all the sporangia of a synangium. In the presence of a central cup at the summit of the synangium it resembles *Cyathotrachus altus* Watson (13). It differs from that species, however, in not having a tracheal cup developed in the basal receptacle. Instead of this, transfusion tissue occupies the short central column as in *Ptychocarpus*, in which, however, the column extends the full length of the sporangia. In the sporangia studied by the writer structural agreement is much closer to *Cyathotrachus*.

The name *Cyathotrachus bulbaceus* is proposed for the species on account of the bulblike shape of the individual synangia. The absence of the tracheal cup, however, may possibly warrant its generic separation from *Cyathotrachus*.

RELATIONSHIPS OF THE ASTEROTHECEAE

STUR (12), in his classification of Culm and Carboniferous ferns, grouped into the suborder Asterotheceae all those forms which he considered to be of Marattiaceous affinities, those in which the sporangia of a sorus are grown together into a more or less globular synangium. The suborder included four genera: *Asterotheca* Presl, *Scolecopteris* Zenker, *Sturiella* Weiss (*Renaultia* Stur), and *Ptychocarpus* Weiss (*Diplazites* Goebb.). To these four there must now be added two others. Practically all paleobotanists have placed the fructifications of *Pecopteris polymorpha* in the genus *Scolecopteris*, although SCHIMPER (10) in 1890 founded the genus *Acitheca* for its reception. In 1925 KIDSTON (6) agreed with SCHIMPER in excluding this species from the genus *Scolecopteris*, a view which in the writer's opinion is justified on the basis of structural differences. In 1906 WATSON (13) described isolated synangia for which he erected the genus *Cyathotrachus*. Brief descriptions of these six genera follow.

Asterotheca.—Synangia sessile, consisting of three to eight exannulate sporangia which are more or less ovate, with the free end brought to a short acute apex. The major axis of the sporangium is usually parallel to the frond which supports it. Dehiscence is by means of a longitudinal slit along the inner margin of the sporangia.

Scolecopteris.—Sporangia united laterally at their bases into a circular synangium which is shortly pedicellate. Sporangia free above, and dehiscing by a longitudinal slit along their inner margin. The long axis of the sporangia is perpendicular to the surface of the frond. The main difference between this genus and the preceding is the presence of a pedicel to the synangium.

Acitheca.—Synangia sessile, usually formed of four (rarely three or five) sporangia. Sporangia exannulate, long, rounded at base, and terminating in a sharp bristle-like point, the upper two-thirds of their length free, the basal third united to a central column. The synangia thus formed are attached by their broad bases perpendicu-

larly to the lower surface of the pinnule. The column or receptacle into which a vascular bundle extends has four plates or wings to which the sporangia are united. Dehiscence takes place through a vertical cleft along the adaxial margin of the sporangia. The margins of the pinnules are recurved and almost cover the synangia.

Sturiella.—Sporangia in groups of five, united below by their fused bases which form a concave plate attached to the pinnule by a short pedicel. The sporangia are described as cylindrical, pyriform, with adjacent sides slightly flattened (9). There is an apical annulus which caps the sporangium and runs down the dorsal wall for some distance toward the base. Dehiscence is by means of a longitudinal cleft along the inner margin of the sporangium.

Cyathotrachus.—The synangium consists of from four to seven sporangia grouped around a central receptacle which is hollowed out into a cup above. The whole is surrounded by a continuous integument. The whole structure was attached to the organ which bore it by a small base. The base apparently received a bundle from the stalk or support, and this bundle spread out into a cup of short tracheids in the sterile tissue at the base of the synangia. The sporangia probably dehisced into the central cup.

Ptychocarpus.—Sporangia almost cylindrical, contracting slightly upward with a truncate apex, attached throughout their entire length to a central column and united to each other laterally, the individual sporangia of the synangium thus formed being inclosed in a common envelope of ground tissue. The synangia are shortly stalked and each consists of from five to eight sporangia. The mode of dehiscence is unknown.

With the exception of *Cyathotrachus*, in which the pinnules are unknown, the shape of the frond in these genera is known to be of the *Pecopteris* type. The sporangia are borne in a double series, one each side of the mid-vein, the attachment of the sporangia being directly over a lateral vein.

It seems reasonable to assume that the primitive state in the *Asterotheceae* was that of groups of separate sporangia, each sporangium being sessile on the leaf. The fusion of individual sporangia into a synangium having a common envelope and the development of a pedicel to the synangium in all probability represent specializa-

tions. *Ptychocarpus* represents the final product of this line of evolution. The accompanying provisional family tree (fig. 38) has been drawn to show the relations among the genera.

PTERIDOSPERMS

Telangium pygmaeum sp. nov. (preparations 545-548)

DIAGNOSIS.—Branching rachis without lamina, bearing synangia terminally or laterally on its ultimate ramifications. Synangia circular, consisting of three to five sporangia which are fused laterally for about one-third their length. Sporangia attached to the rachis by a broad base, ovoid in shape, measuring 0.6 mm. by 0.19 mm. Spores circular, 35 μ in diameter, smooth, and marked with a tri-radiate ridge.

Preparations 545 to 548 contain small exannulate sporangia grouped into circular synangia. These are attached to a badly preserved rachis which does not appear to be a foliage leaf (figs. 16, 30). The walls of the sporangia appear to be but one layer of cells in thickness. The sporangia are fused laterally for the basal one-third to one-half of their length. For the attachment of the terminal synangium the rachis is expanded. Other synangia are attached laterally to the same rachis by a broad area of attachment. The synangia are distinctly sessile.

Digitate clusters attached to branching petioles devoid of lamina, and associated with or attached to leaves of the *Sphenopteris* type, have been known for a great many years as plant impressions from Paleozoic rocks. These were first investigated by STUR (11) who gave to them the name *Calymmatotheca*. *C. stangeri* is the type species of the genus. STUR considered the constituent parts of the digitate clusters as indusial bracts, but RENAULT considered them to be sporangia.

These two conflicting opinions were held until BENSON (1) obtained petrifications of sporangia which led her to make a careful re-investigation of STUR's type specimens of *Calymmatotheca*. She concluded that STUR's interpretation as to the nature of his specimens was correct, and that the sporangia would have to be excluded from that genus. The form genus *Telangium* with *T. scotti* as the type species was erected for these sporangia.

BENSON (1) gives the following diagnosis for the genus *Telangium*:

Fertile and barren pinnae dissimilar; fertile pinnae represented by synangia only; synangia borne at the extremity of the ultimate ramifications of the rachis, composed of six to twelve sporangia which taper to the apex and are united primarily for almost their whole length to form a body which is continued into a sterile base of decreasing diameter through which runs longitudinally a single vascular strand. Each sporangium ultimately becomes almost free from the others by septicidal dehiscence and liberates large spores from a ventral suture.

One species with structure preserved, *T. scotti*, was described by BENSON. Several other species, based upon impressions only, have also been placed in this genus.

The following is a list of the previously known species:

T. scotti Benson, from the Gannister beds of Lancashire.

T. affine L. & H. and *T. bifidum* L. & H., both from the Calciferous Sandstone series of England.

T. digitatum Kidston from the Lanarkian of England.

T. nutans Carpentier from the Upper Carboniferous of France.

The fertile frond of *Sphenopteris potieri* may prove to be a *Telangium*. It is found in the Upper Carboniferous of France and also from the Staffordian of England. *T. asteroides* Lesq. has proved to be an imperfect specimen of *Crossothea hoeningshausii*, and must therefore be dropped from the list of species of *Telangium*.

As the Illinois specimens are very much smaller than any of those previously described, the name *Telangium pygmaeum* is proposed. *T. pygmaeum* is sharply separated from the other species of *Telangium* both by its smaller size and also by the smaller number of sporangia making up a synangium. The sporangia measure only a little more than 0.5 mm. in length, whereas *T. affine*, the smallest of the previously described species, measures 2.5–3. mm., and *T. digitatum*, the largest, has a synangium composed of about 25 sporangia which attain a length of 8 mm. *T. pygmaeum* occurs considerably later in geologic time than the other species.

Conostoma platyspermum sp. nov. (preparations 501–516)

DIAGNOSIS.—Seed platyspermic, ribs absent, seed sometimes slightly 2-angled. Integument and nucellus undiverged at plinth level. Vascular strands two, in the inner region of the integument, each corresponding to an angle of the seed. Size ranges up to 4.5 mm. in length by 2.5 mm. in width by 2.0 mm. in thickness.

The genus *Conostoma* was founded by WILLIAMSON (14) in 1887. It included three species of small Paleozoic seeds: *C. oblongum* from the Gannister beds of the Lancashire coal fields, and *C. ovale* and *C. intermedium* from the Calciferos Sandstone series of Burntisland, Scotland. The latter two species were re-investigated by BENSON, however, who reduced them to one; and, in view of its structural differences, removed it from the genus *Conostoma* and made it the type of a new genus, *Sphaerostoma*. In 1911 OLIVER and SALISBURY (8), having new and more abundant material available, restudied *Conostoma*. *C. oblongum* was redescribed in greater detail, and a new species, *C. anglo-germanicum*, was founded on material from Shore, Littleborough, England, and from Duisburg in Rheinpreussen, Germany. KRICK (7) has also described *C. oblongum* from coal ball material from coal no. 5 at Harrisburg, Illinois.

In the study of coal ball material from Calhoun, a related but undescribed species of seed came to light. The seed is represented by a number of specimens, all found in the same coal ball, but without any organic connection between them and any other material. In view of the pronounced platyspermic nature of the seed it is proposed that the new species be called *Conostoma platyspermum*.

OLIVER and SALISBURY (8) give the following diagnosis of the genus *Conostoma*:

Cylindrical or slightly flattened seeds with tapering insertion. Ribbed throughout, or at base with angles passing into ribs. Lobing at apex variable; vascular bundles equalling or fewer than the ribs or angles; loculi of canopy nearly obliterated and equalling the vascular bundles in number; epidermis mucilaginous. Lagenostome very small, included; cells of wall sculptured. Plinth conspicuous, dome shaped, with internal tissue; well marked "tent pole" and tapetum present.

The Illinois specimens agree in all essential features with this generic diagnosis, and are thus included in the genus *Conostoma*.

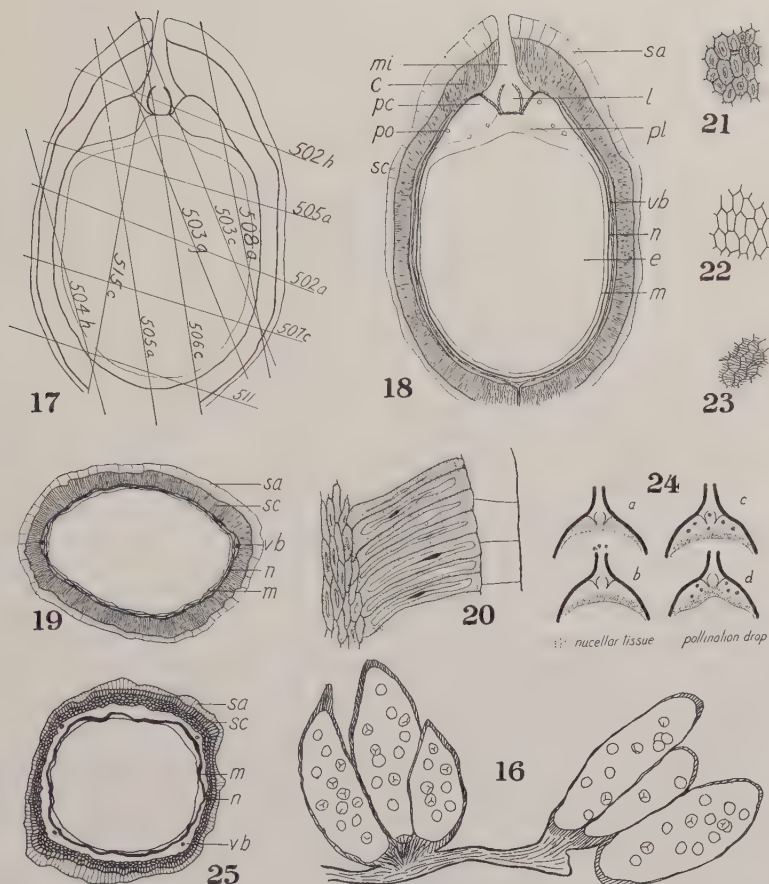
The new species differs from *Conostoma oblongum* and *C. anglo-germanicum* in being distinctly platyspermic, although *C. oblongum* in some measure shows this feature. In cross-section the seed is elliptical in outline. In all three of the specimens of which transverse sections are at hand (preparations 502, 505-512, 513) the flattening is parallel to the plane in which the two vascular bundles lie (principal plane of the seed), so that such flattening can scarcely be ascribed

to deformation of the seed (fig. 19). In longitudinal section the seed is somewhat oblong, with more or less parallel sides (figs. 18, 32, 33), but the whole structure is relatively shorter than that of *C. oblongum* and *C. anglo-germanicum*. An interior mold of the seed is shown in figure 31.

The new species has a single integument and the nucellus is undiverged to near the summit of the latter. The integument has a characteristic structure, making it easy to recognize various sections of the seed as belonging to the same species. It is composed of three distinct layers: a sarcotesta; a middle layer or sclerotesta; and an inner layer of delicate tissue, for the most part not preserved, but which must have surrounded the nucellus and in which the vascular bundles ran. In some cases the greater part of the thin sarcotesta has been lost by exfoliation, from which habit OLIVER and SALISBURY gave to it the name "blow-off" layer in their description of *C. oblongum*. The sclerotesta is variable in thickness, depending on the seed and on the plane of section. In the body of the seed its thickness is 0.1–0.23 mm. At the summit the integument becomes much thickened to form a conical canopy surrounding the micropyle.

The nucellus measures about three-fourths the length of the seed. It is non-diverged from the integument for its whole length (fig. 18). At the summit there is a large pit or depression, from the floor of which the small lagenostome arises. The lower portion of the nucellus is replaced by the growth of the megagametophyte (endosperm), the megaspore membrane marking the contact of the two structures. Only faint and indefinite traces of nucellar and megagametophyte tissues are preserved, excepting the tapetal layer of the nucellus surrounding the latter. The part of the nucellus above the megagametophyte is known as the plinth. The summit of the plinth is occupied by a plinth cavity which functioned as a pollen chamber.

The hard part of the testa which gives the shape to the seed is elliptical in cross-section, cylindrical, and tapering with a steep curve toward the micropyle, and curving more sharply to the chalaza at the other. Thus the longitudinal section of the seed has the characteristic boat shape of *Conostoma*, the micropylar end representing the prow and the chalaza the stern. The length of the seed varies from 1.6 to 2.6 mm. in the measured longitudinal sections; but if the seed



FIGS. 16-25.—Fig. 16, *Telangium pygmaeum*: two synangia attached to a rachis (546). $\times 44$. Figs. 17-24, *Conostoma platyspermum*: 17, diagrammatic sketch of median longitudinal section of seed plotting approximate positions of chief sections used in this paper; 18, reconstructed longitudinal section (c, canopy; e, megagametophyte [endosperm]; l, lagenostome; m, megaspore membrane; mi, micropyle; n, tapetal layer of nucellus; pc, plinth cavity or pollen chamber; pl, plinth; po, pollen grains; sa, sarco-testa; sc, sclerotesta; vb, vascular bundle). $\times 11$; 19, cross-section (508a). $\times 11$; 20, semi-diagrammatic drawing of radial section of testa showing sarcotesta and the two zones composing sclerotesta. Note shrunken protoplasm in prismatic cells (514). $\times 93$; 21, tangential section of same. $\times 93$; 22, tangential section of epidermis of plinth (515c). $\times 93$; 23, tangential section of wall of lagenostome showing sculptured cells (506). $\times 93$; 24, diagrammatic representation of summit of seed showing development of pollen chamber and method of pollination. Fig. 25, cross-section of seed of *C. quadratum* (518b), legend as in fig. 18. $\times 22$.

shown in cross-section in figures 19 and 49 has the same relative proportions, its length must be about 4.5 mm. In transverse section the seeds show their platyspermic nature. Preparation 502 (fig. 34) measures 1.5 by 0.9 mm., maximum and minimum diameters, and the other specimen (507c, fig. 19) measures 2.5 by 2.0 mm. In both cases the flattening was in the plane of the seed which includes the two vascular bundles. In the first specimen the sclerotesta is somewhat thickened above the vascular bundles, but the other shows no indication of increased thickness. In no case were there any ridges in the testa such as is characteristic of *C. oblongum* and *C. anglo-germanicum*.

The internal form of the testa is, in the main body of the seed, similar to the exterior. The summit is dome-shaped, however, and passes into the funnel-like lower end of the micropyle. At the apical end of the seed the testa is markedly thickened to form the canopy.

The integument consists of three distinct zones. From the exterior inward they are: the sarcotesta, the sclerotesta, and a delicate thin walled zone through which the vascular bundles progress. The sarcotesta consists of a single layer of light colored cells investing the external surface of the seed. At the apex the cells of this layer are much enlarged to form a fleshy cap to the seed. The length of these cells is 160 μ , which is in contrast to the thickness of about 40 μ for the sarcotesta of the remainder of the seed.

There is some doubt as to the true shape of the apical end of the seed. In two specimens (503-504 and 505-512) the seed appears to be truncated abruptly, the enlarged epidermal cells forming a cylinder surrounding a wide and squarely truncated canopy (figs. 32, 35). In 515c (fig. 33) the canopy appears to be of the more nearly normal dome shape, however, with the sarcotesta reaching to its summit and surrounding the micropyle. The writer is inclined to the view that the truncated appearance of the other specimens is due to destruction of tissue prior to fossilization. He has therefore shown a complete sarcotestal cap in his reconstruction (fig. 18).

As its name implies, the sclerotesta is made up of sclerotic, thick walled elements, its thickness varying from 0.1 to 0.23 mm. in various seeds. There are two distinct layers of tissue making up the sclerotesta (fig. 20). The outer layer consists of a single series of

palisade cells, the inner of elongated sclerotic cells disposed longitudinally. The amount of this tissue is variable; in some cases the palisade layer constitutes most of the integument, in others the longitudinally elongated elements make up one-third of the thickness. The cells of the prismatic layer are roughly hexagonal in cross-section (fig. 21). The cells are extremely thick walled and have a narrow lumen. The shriveled protoplasmic contents (fig. 20) show as black specks, and give to the integument, as seen in section, a peculiar peppered appearance.

A single vascular bundle enters the chalazal end of the seed, and after penetrating to the inner layers of the integument, divides into two. These branches are in the plane of the major diameter of the seed, and lie in the inner layers of the integument, just outside the nucellus. Whether they extend into the canopy could not be determined from the specimens, but by analogy with *Conostoma oblongum* it is probable that they do. As seen in cross-section, the individual bundle consists of about eight or nine tracheids exhibiting scalariform thickenings (fig. 34).

The nucellus falls into three regions: (1) the lagenostome, which arises from the base of a cuplike depression at the summit of (2) the plinth or distal portion of the nucellus, and (3) the main part of the nucellus, now almost completely replaced by the growth of the megagametophyte within it. The nucellus is undiverged from the integument except for the cuplike depression at the summit of the plinth, and for the lagenostome. This differs from the two previously described species in which the nucellus was free from the integument at the level of the plinth.

The body of the nucellus has been almost completely replaced by the growth of the megagametophyte, whose limits are marked by a brown line representing the megaspore membrane. Only in one specimen (section 514) is there any gametophyte tissue preserved, and in this the preservation is extremely poor. All that can be distinguished are a few delicate parenchyma cells. Of the nucellus only the tapetal layer remains, and this is crowded between the megagametophyte and the integument. This tapetal layer consists of extremely large flattened cells of polygonal outline (fig. 36), measuring about $150\ \mu$ in diameter by $40\ \mu$ in thickness.

LAGENOSTOME AND PLINTH.

These two organs, which form the summit of the nucellus, are so intimately related that they may most conveniently be dealt with together. The distal portion of the plinth is occupied by the plinth cavity (fig. 18 *pc*). The proximal portion of the plinth was occupied by nucellar tissue. With the exception of a plug of crushed tissue at the base of the lagenostome, none of this tissue is preserved, but the boundary between this and the plinth chamber is marked by a faint brown line. Apart from these remains of internal filling tissue, the plinth is represented only by the epidermis which, where its structure is well enough preserved, is seen to consist of a single layer of flattened epidermal cells without special sculpturing (fig. 22).

Following the epidermis of the plinth down the slope of the cup at its summit, it becomes evaginated to form the lagenostome. Thus the epidermis of the plinth and of the lagenostome is one continuous structure. The lagenostome, as in *Conostoma oblongum*, is a tiny goblet-shaped body, the cavity of which communicated with the plinth cavity at the time of pollination. Unlike *Physostoma* and *Lagenostoma*, the mouth is unprovided with any tube or beak. Although none of the specimens studied shows it, by analogy it seems probable that the mouth engaged with the micropylar tube by means of a bevelled flange such as is found in *C. oblongum*. The lagenostome measures $170\ \mu$ in maximum diameter by about $150\ \mu$ in height (fig. 35). The wall of the lagenostome is formed of a single layer of cells which have an elaborate tracheid-like sculpturing (fig. 23). The floor of the lagenostome does not consist of differentiated sculptured cells but is occupied by a pad of crushed nucellar tissue, the individual cells of which are for the most part indistinguishable. The formation of this pad will be discussed later in connection with the method of pollination. The plinth chamber (fig. 18) lies at the very summit of the nucellus. It is annular in shape and approximately triangular in cross-section. It is bounded on the inside by the epidermis of the depressed cup at the summit of the nucellus; on the outside by the undiverged nucellus and integument; and below by nucellar tissue. This plinth cavity functioned as a pollen chamber, and it is within this cavity that the pollen is nearly always found. In only one case (fig. 3) was any pollen found in the lagenostome.

The pollen grains are multicellular, elliptical in form, and measure 50 by 65 μ in diameter. In common with other Paleozoic seeds there is no evidence of the development of pollen tubes. The absence of pollen tubes and of embryos in Paleozoic seeds may possibly both be due to the same cause, namely, that the "seeds" so far studied are really ovules. The fact that the integument is made up of thick walled stony cells is not incompatible with this view, since in modern gymnosperms, as in the cycads and some conifers, the integument may have become sclerotic before the archegonia are developed.

An outline of the probable course of events in the history of ovular maturation and pollination will help in understanding the relationships of the various parts. At an earlier stage of development than any represented by the preparations, the tip of the nucellus must have been occupied by a soft internal tissue which filled the lagenostome and the plinth, the tissue being continuous from one to the other through the narrow orifice by which these structures communicated (fig. 24 *a*). As the time of pollination drew near, the filling tissue of the lagenostome and the summit of the plinth doubtless underwent degeneration (fig. 24 *b*). A pollination drop was exuded at this time. It was probably formed in part by the mucilaginous substances resulting from disintegration of the internal tissues of the lagenostome and plinth, and in part by secretion from the tracheid-like sculptured cells which make up the walls of the lagenostome. The pollen was caught by this exuded drop, which, as it dried, carried the pollen grains through the lagenostome into the plinth chamber (fig. 24 *c*). The plinth cavity was then closed by the growth of the "tent-pole" of the megagametophyte. This forced the overlying nucellar tissues against the base of the lagenostome, thus sealing the opening (fig. 24 *d*).

Two species have previously been described, *Conostoma oblongum* and *C. anglo-germanicum*. *C. platyspermum* shows more features in common with the former species. In its general proportions and the relation of its height to width, it bears a much stronger resemblance to the former; indeed, in proportion to its length it is even broader than that species. Also, in its platyspermy and in the absence of ridges or wings it resembles *C. oblongum* more closely. In the reduced number of vascular bundles, however, it shows agree-

ment with *C. anglo-germanicum*, and with *Gnetopsis elliptica*, another seed belonging to the *Conostoma* group. In view of the platyspermic nature of *C. oblongum*, *C. platyspermum*, and *Gnetopsis elliptica*, it is interesting to note that in *C. oblongum* there are six vascular bundles, one beneath each of the two major angles of the seed and four intermediate bundles. In *Gnetopsis* the bundles corresponding to the major angles have been lost. In *C. platyspermum*, on the other hand, only the two bundles corresponding to the major angles of the seed are present.

***Conostoma quadratum* sp. nov.** (preparations 517-519)

DIAGNOSIS.—Seed squarish in cross-section. Ribs absent. Radi-spermic with four vascular bundles. Diameter 1.35 mm.

A number of closely spaced transverse sections of a small seed were obtained by the film method from coal ball C 237. Only the basal portion of the seed is known, as the apical portion was lost in the primary saw cut.

The seed is extremely small, measuring only 1.35 mm. in diameter. The general arrangement of its tissues (figs. 25, 37) is that of a member of the *Conostoma* group. The integument consists of a sarcotesta comprising a single layer of epidermal cells, and a sclerotesta comprising an outer prismatic zone and an inner non-prismatic zone. Four vascular bundles, each corresponding to a corner of the seed, run longitudinally in the now empty space between the integument and nucellus. In the cross-sections the nucellus appears to be free from the integument, owing partly to shrinkage and partly to disintegration of the delicate tissue which formed the innermost part of the integument. The loss of tissue makes it appear as if the nucellus were free from the integument. The same appearance is seen in cross-sections of *C. platyspermum* but in that case the longitudinal sections leave no doubt at the non-divergence of the nucellus and integument. The limits of the megagametophyte are defined by the megaspore membrane. The testa is variable in thickness, measuring 90-180 μ . This variation bears no relation to the vascular strands nor to the symmetry of the seed (figs. 25, 37).

The sarcotesta is relatively more extensive than in the other species of *Conostoma*, as it makes up one-third to one-half the thickness

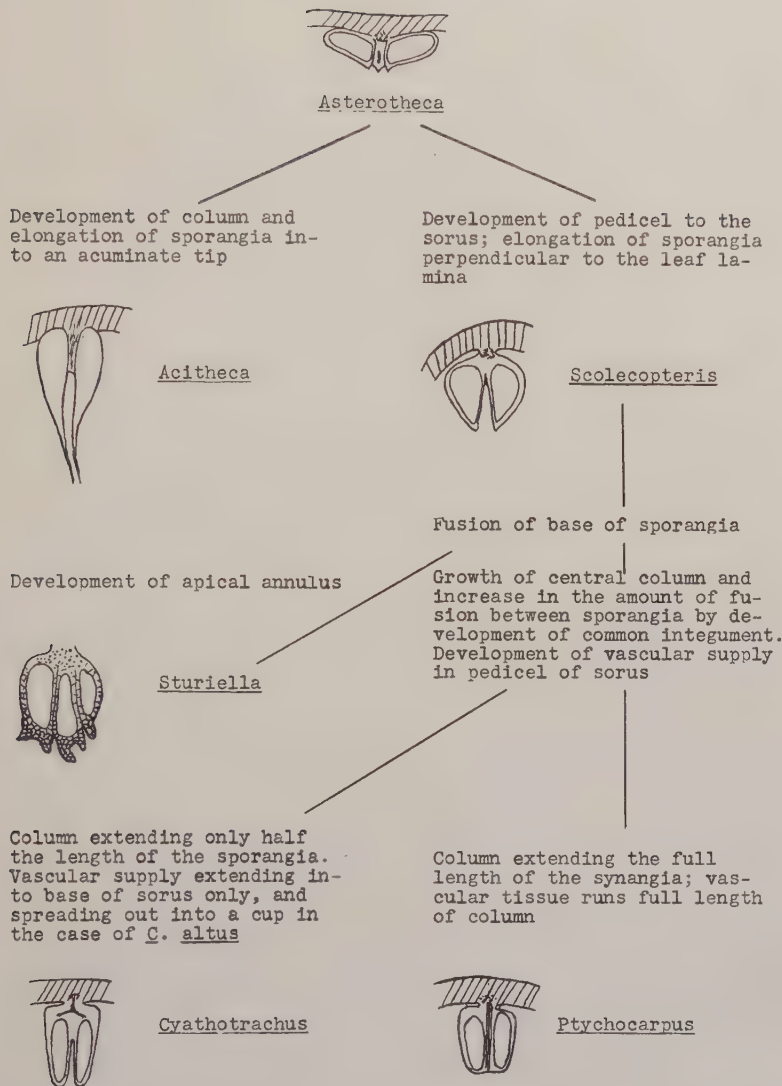


FIG. 38.—Provisional family tree showing relations among genera of the Asterothecaceae.

of the testa, and there appears to be no tendency for it to be exfoliated. The sclerotesta consists of two zones, a prismatic zone on the outside and a non-prismatic one on the inside. The prismatic zone is made up of a single layer of stout cells averaging $20\ \mu$ in diameter and $40\text{--}50\ \mu$ in length. The inner zone of the sclerotesta is made up of what appears in transverse section to be isodiametric thick walled cells. By analogy with those of closely related seeds, these cells probably are really longitudinally elongated.

The four vascular bundles are found at the corners of the seed in the empty space lying between the sclerotesta and the nucellus. In some places there are slight traces of a delicate parenchyma which formerly occupied this space. Each vascular bundle consists of about twelve minute tracheids, approximately $3\ \mu$ in diameter. The type of tracheal sculpturing could not be resolved very well but it appeared to be scalariform. The sections at the chalaza show that a single vascular bundle enters the seed and passes into the inner layers of the integument, where it divides to give rise to the four bundles.

Only the tapetal layer of the nucellus is preserved. It consists, as in *Conostoma platyspermum*, of the large platelike polygonal cells. The megaspore membrane is for the most part in contact with this layer. Where this is not the case, the condition is probably due to shrinkage. No endosperm is preserved.

The undiverged nucellus, and the fact that the vascular bundles run in the innermost region of the integument, place this seed in the group Lagenostomales. Unfortunately micropylar sections are lacking, so that the most characteristic structures on which the classification of this group is based are absent. However, the structure of the integument is that typical of the Conostomae (7). In this group there are but two genera, *Conostoma* and *Gnetopsis*, and the similarity of the latter genus to the former may possibly warrant its inclusion in *Conostoma*. In view of this fact, this seed is assigned there provisionally. The discovery of other specimens showing the micropyle and lagenostome will of course be necessary to confirm this classification. Having regard to the squarish cross-section of the seed, the name *Conostoma quadratum* is proposed.

As far as limited material permits one to say, *C. quadratum* agrees

more closely with *C. anglo-germanicum* than with any other species. In common with that species, the sarcotesta is more extensive and persistent than in the other species. It also agrees in having radial symmetry and four vascular bundles. It differs markedly from that species in the entire absence of ribs, and it is much smaller in size. In the absence of ribs it shows agreement with *C. platyspermum*, from which, however, it differs markedly in other respects, as in general shape of the seed and in the histological structure of the integument (cf. figs. 19 and 25).

Summary

1. A morphological study was made of plant material preserved in coal balls from Calhoun coal mine, Richland County, Illinois. The geologic horizon is Middle Conemaugh, early Upper Pennsylvanian.

2. Preparations were made by the cellulose peel method.

3. Seven plants are described in detail. Of these, four are sporangia of ferns, one is the microsporangium of a pteridosperm, and two are seeds. The plants described are: *Notoschizaea robusta* gen. et sp. nov., *Scolecopteris latifolia* sp. nov., *Scolecopteris minor* Hoskins, *Cyathotrachus bulbaceus* sp. nov., *Telangium pygmaeum* sp. nov., *Conostoma platyspermum* sp. nov., and *Conostoma quadratum* sp. nov.

4. A short discussion of the ferns belonging to the Asterotheceae is given, with a phylogenetic tree showing probable relationships.

5. It is suggested that the absence of tubes in the pollen found in the pollen chambers of Paleozoic seeds and the absence of embryos may possibly be due to the same cause, namely, the fact that the so-called seeds are really immature ovules.

UNIVERSITY OF CAMBRIDGE
CAMBRIDGE, ENGLAND

LITERATURE CITED

1. BENSON, M., *Telangium Scotti*, a new species of *Telangium* (Calymmatotheca) showing structure. *Ann. Botany* 18:161-167. 1904.
2. BERTRAND, P., L'étude anatomique des fougères anciennes et les problèmes qu'elle soulève. *Progressus rei Botanicae* 4:255-256. 1913.
3. GRAHAM, ROY, Preparation of palaeobotanical sections by the peel method. *Stain Technology* 8:65-68. 1933.
4. HIRMER, M., *Handbuch der Paläobotanik*. vol. I. 1927.

5. HOSKINS, J. H., Structure of Pennsylvanian plants from Illinois. BOT. GAZ. 82:427-436. 1926.
6. KIDSTON, R., Fossil plants of the Carboniferous rocks of Great Britain. Mém. Geol. Surv. Great Britain. Paleontology. vol. II. pt. 6. 1925.
7. KRICK, HARRIETTE V., Structure of seedlike fructifications found in coal balls from Harrisburg, Illinois. BOT. GAZ. 93:151-172. 1932.
8. OLIVER, F. W., and SALISBURY, E. J., On the structure and affinities of the *Conostoma* group of Palaeozoic seeds. Ann. Botany 25:1-50. 1911.
9. RENAULT, B., Cours de botanique fossile. vol. III. 1883.
10. SCHENK, A., and SCHIMPER, W. P., in ZITTEL: Handbuch der Palaeontologie Abth. 2. Palaeophytologie. p. 91. 1890.
11. STUR, D., Die Culm-flora. Abhandl. K. K. Geol. Reichsanstalt. Heft II. 1877.
12. ———, Zur Morphologie und Systematik der Culm- und Carbonfarne. Sitzb. der Math.-Naturw. Classe der K. Akad. der Wissensch. Wien. Abt. I. 88:704-778. 1884.
13. WATSON, D. M. S., On a "fern" synangium from the lower Coal Measures of Shore, Lancashire. Jour. Roy. Microscop. Soc. pp. 1-3. 1906.
14. WILLIAMSON, W. C., On the organization of the fossil plants of the Coal Measures. Part 8. Phil. Trans. Roy. Soc. London B. 167:213-270. 1877.

EXPLANATION OF PLATES VIII, IX

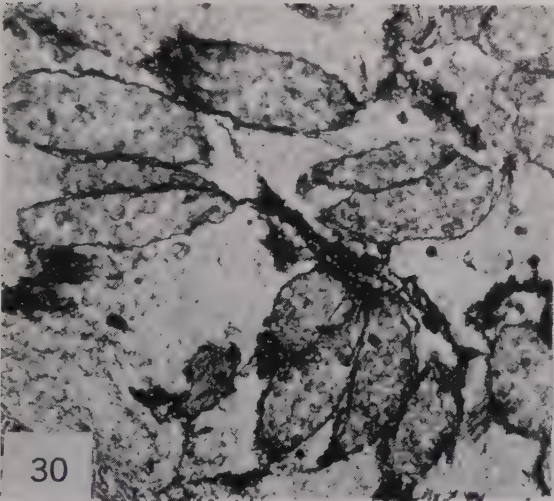
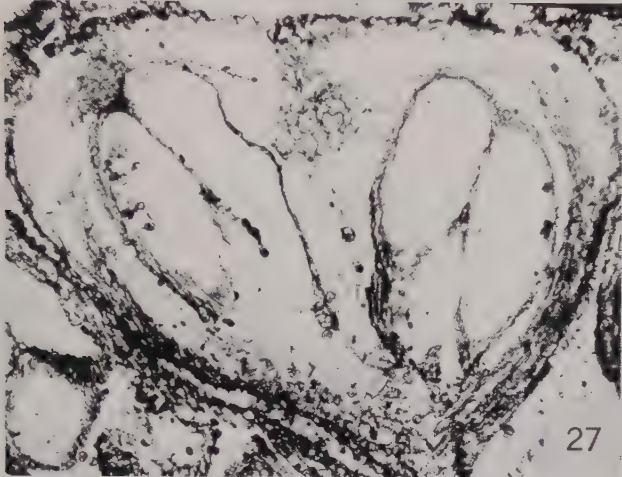
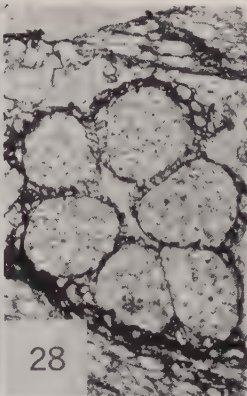
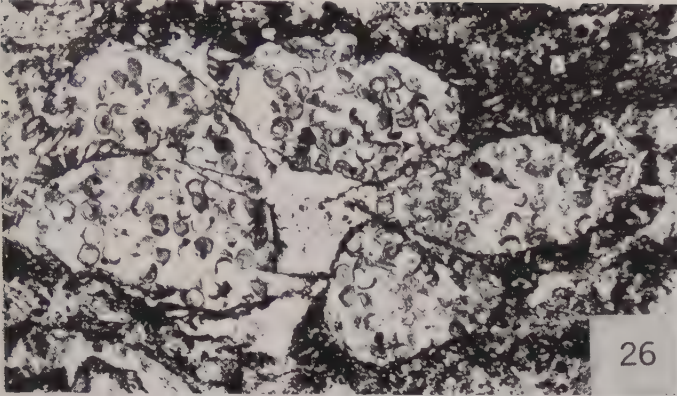
PLATE VIII

- FIG. 26. *Notoschizaea robusta*: transverse section of sorus (552a). $\times 50$.
 FIG. 27. *Scolecopteris latifolia*: cross-section of pinnule (543b). $\times 37$.
 FIG. 28. *Cyathotrachus bulbaceus*: transverse section of synangium (540). $\times 55$.
 FIG. 29. Longitudinal section of synangium of same (541c). $\times 55$.
 FIG. 30. *Telangium pygmaeum*: two synangia in longitudinal section attached to rachis; other synangia cut obliquely (546). $\times 45$.
 FIG. 31. *Conostoma platyspermum*: internal cast of seed (*pl*, plinth; *tp*, "tent-pole" or beak of endosperm) (501). $\times 33$.

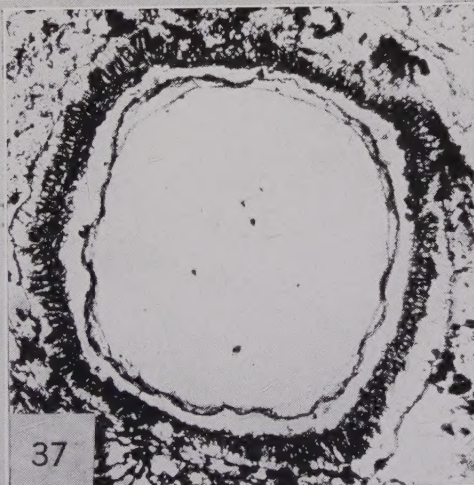
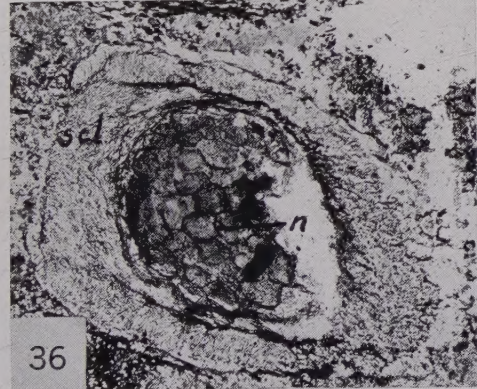
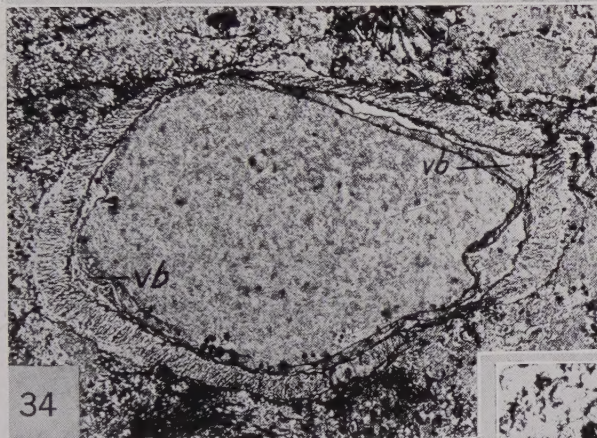
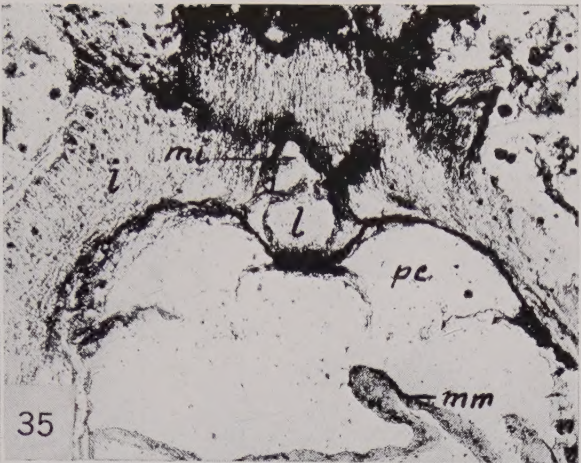
PLATE IX

Conostoma platyspermum

- FIG. 32. Obliquely longitudinal section of seed (503f). $\times 30$.
 FIG. 33. Same showing complete canopy (515). $\times 30$.
 FIG. 34. Transverse section showing vascular bundles (*vb*) (502b). $\times 33$.
 FIG. 35. Longitudinal section of apical portion of seed (*i*, integument; *l*, lagenostome; *mi*, micropyle; *mm*, megaspore membrane; *pc*, plinth cavity) (506c). $\times 60$.
 FIG. 36. Tangential section showing sclerotesta (*scl*) and tapetal layer of nucellus (*n*) (504h). $\times 30$.
 FIG. 37. *Conostoma quadratum*: cross-section of seed. $\times 50$.



GRAHAM on PENNSYLVANIAN FLORA



GRAHAM on PENNSYLVANIAN FLORA

